THE PHYLOGENETIC POSITION OF
CHLORONIELLA PERINGUEYI
(MEGALOPTERA: CORYDALIDAE)
AND ITS ZOOGEOGRAPHIC SIGNIFICANCE[1]

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ABSTRACT: Male and female genitalia of *Chloroniella peringueyi* are illustrated for the first time, and phylogenies of all genera of Corydalinae are presented, based both on morphological analysis and plate tectonics. A possible general pattern of megalopteran evolution is suggested.

When Glorioso (1981) published his revision of the Corydalinae, he did not include the South African genus *Chloroniella* in his phylogenetic analysis because he was "unable to obtain specimens of the only known species due to its scarcity in collections." Further attempts to locate additional specimens by the present author have also been unsuccessful. In November 1986 Drs. John T. Doyen and Charles E. Griswold collected 14 specimens of a species that compares well with the original description of *Chloroniella peringueyi* Esben-Petersen at Algeria Forest Camp in the Sederberg mountains of Cape Province, South Africa. Thus, the time seems appropriate to revise the original cladistic analysis to include all known genera.

METHODS

The cladistic analysis utilized the 70 character states from Glorioso's study with a few modifications. His character 18, the stipal setae, was found to be too variable for inclusion. Characters 30 and 41, the 1A branches and male ninth sternal setae respectively, were not included in his cladogram, but are included here. His first three character states are common to all Corydalinae, and thus are uninformative about relationships within the subfamily and have not been included. Five additional characters have been found and are incorporated, four of them exist in *Chloroniella,* two of them being unique to this genus (Table 1). Three of these new characters are autapomorphies[3] within the subfamily, and two are shared with only one other genus. As in Glorioso's study, the apomorphic state was derived from a comparison with genera in Chauliodinae, these being considered the outgroup. In all, 71 charac-

[3] Autapomorphies are also uninformative about relationships, but do provide evidence about the monophyly of a group.
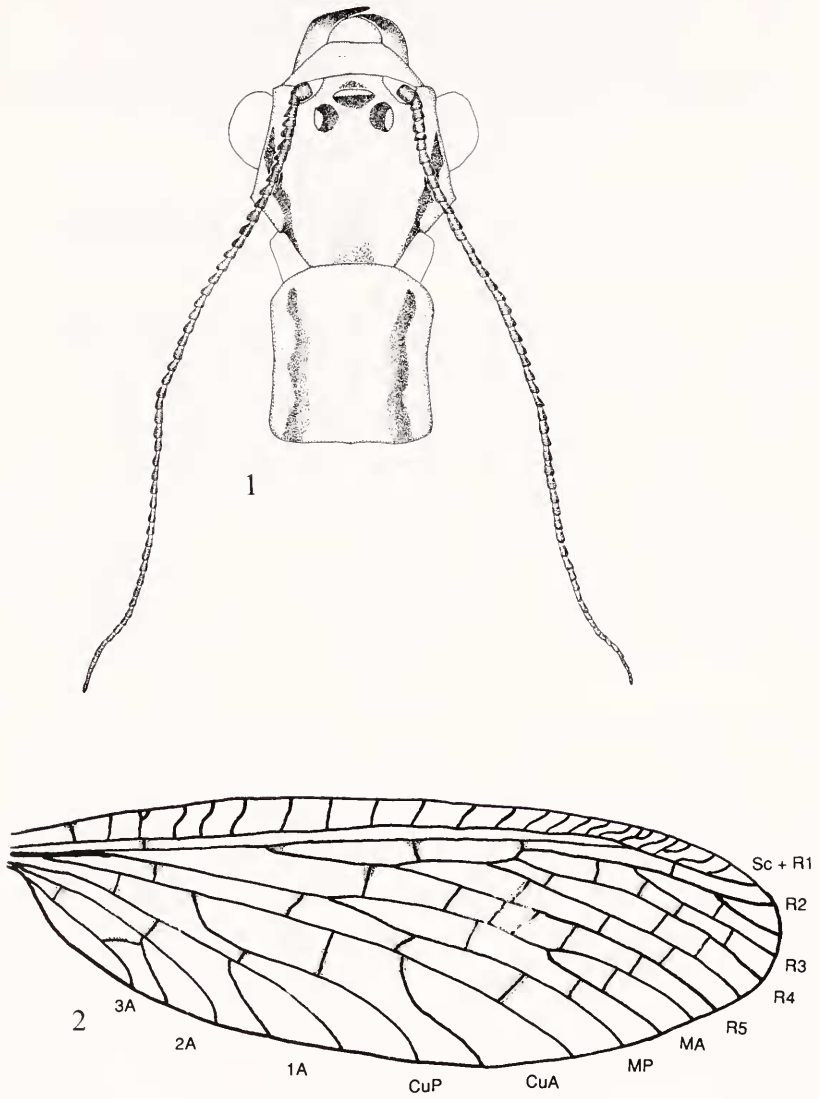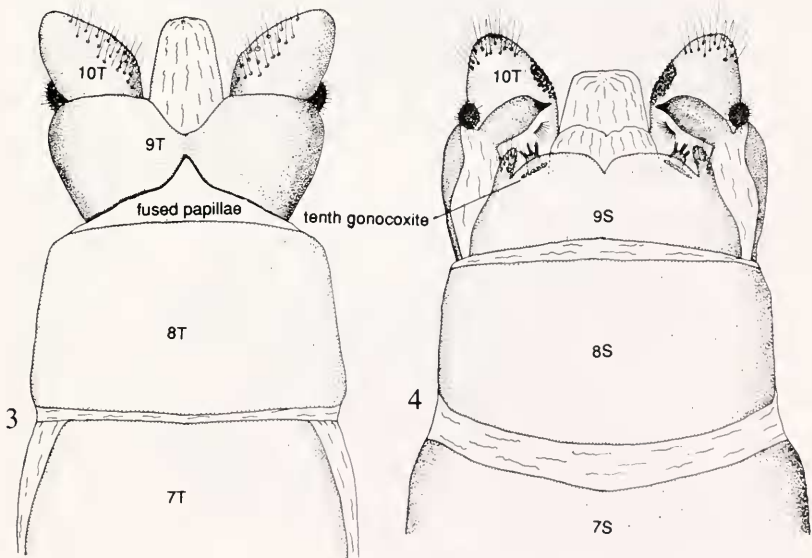
Figures 1-2. *Chloroniella peringueyi*. 1. Head in dorsal view (10X). 2. Right forewing (5X).

ters are considered in this analysis. To help construct the most par-
simonious cladogram, the PAUP computer program was used. Illus-
trations were made utilizing a Wild M6 binocular microscope with a
camera lucida attachment. Genitalia were studied after clearing in 10%
cold KOH for 24 hours and female genitalia were stained with Chlorazol
Black E. The terminology is the same as that used by Glorioso.

RESULTS

Individuals of *Chloroniella* have forewings with mostly plesio-
morphic character states, although a few apomorphic modifications
have arisen, such as reduced apical forks of R5 and MP (Fig. 2). The male
genitalia (Figs. 3, 4) provide the most distinctive characters, with
medially notched ninth sternum, medially fused papillae, a tuft of setae
at the base of the tenth tergites, and medially divided tenth gonocoxites.
Other useful characters are found in the female genitalia (characters 62
to 71) (Figs. 5, 6). The pale coloration with dark markings of *Chloroniella*
superficially resembles that of the New World *Chloronia* and the Asiatic
Neuromus (Fig. 1). Utilizing these and the other characters listed by
Glorioso, only one most parsimonious cladogram is generated by the

Figures 3-4. *Chloroniella peringueyi* apex of male abdomen (25X). 3. Dorsal view. 4.
Ventral view.

PAUP program (Cladogram 1), with a consistency index of 0.688. This cladogram has 109 steps.

CONCLUSIONS

The cladogram generated by PAUP is very similar to that presented by Glorioso. Except for the addition of *Chloroniella*, there are no other changes.

Megalopterans are today highly dependent on fresh water and there is no reason to believe that previous ancestors behaved differently. Adults are heavy-bodied, weak flyers and are seldom found far from streams and lakes. Eggs are laid in large masses on land, and pupae are
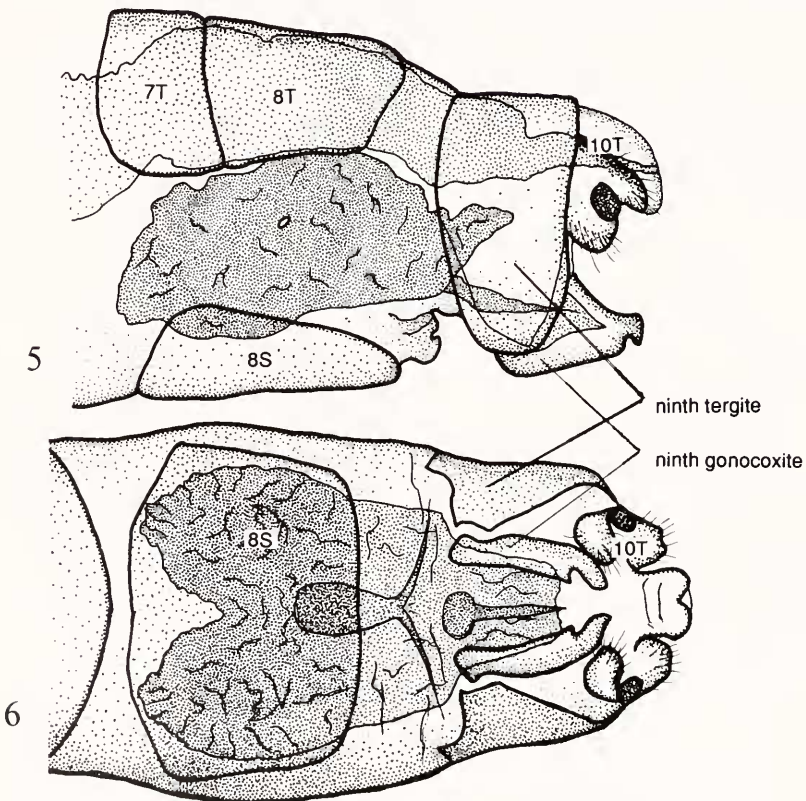
Figures 5-6. *Chloroniella peringueyi* apex of female abdomen (25X). 5. Lateral view. 6. Ventral view.

found on land in the substrate near the margins of water courses. Larvae of all megalopterans are aquatic, and with the exception of Pacific Coast *Neohermes* and *Protochauliodes* are all confined to permanent bodies of water. Thus, the ability to disperse is highly restricted, and present day distribution patterns probably closely reflect past climatic and plate tectonic events. Ancestral forms in Laurasia and Gondwanaland would have suffered drastic distributional and richness reductions as "continental effects produced extensive aridity as the land-mass drifted
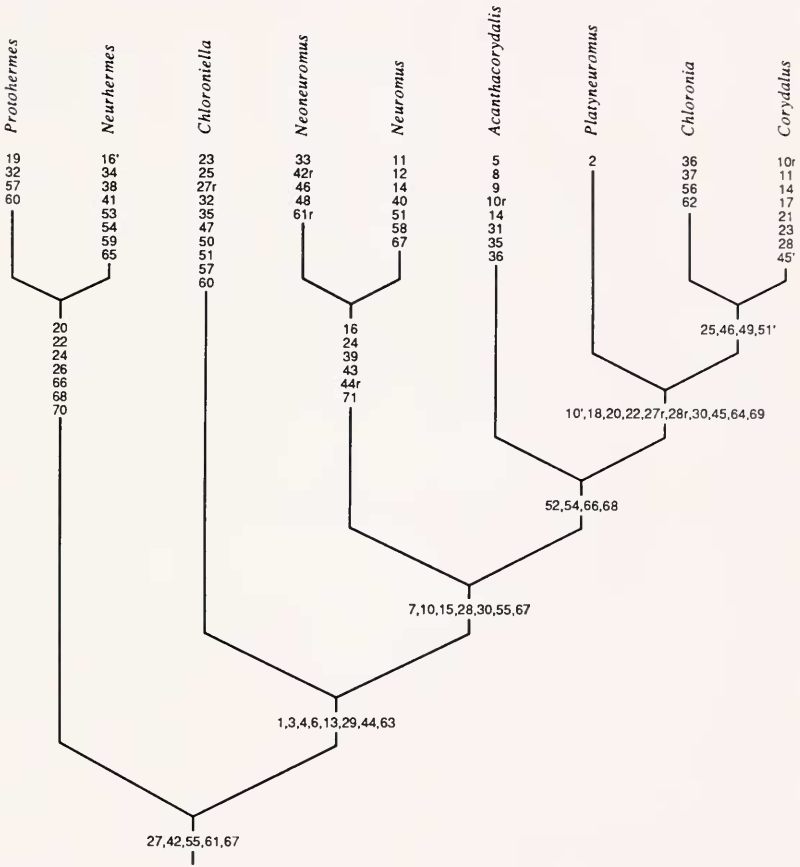
CLADOGRAM 1

Cladogram 1. Phylogenetic position of corydaline genera using PAUP analysis. Numbers refer to apomorphic states in Table 2.

through middle latitudes in the late Permian and Triassic" (Riek, 1970). There would have been a polarizing effect during the Triassic as "the lower-latitude zone featured high aridity to about 45°N and 55°S, except in western Europe, where somewhat greater humidity characterized the higher latitude areas" (Frakes, 1979). At the same time, where aquatic habitats continued to exist, the ameliorating local environment may have allowed primitive forms to survive long after terrestrial forms became extinct. Subsequent improving climatic conditions in lower latitudes during the Paleogene (65 to 22.5 mya) would have allowed plates, such as South America and India, drifting into the tropical zones, to retain and even expand their high latitudinal faunas, while these same faunas were being eliminated closer to the poles—"an abundance of atmospheric moisture at high latitudes seems to have retreated equatorward through the interval, and the first glaciers since the Paleozoic formed and expanded in Antarctica" (Frakes, loc. cit.).

The three suprageneric groups of Megaloptera (Sialidae, Chauliodinae and Corydalinae) all show elements of a previous austral distribution (Maps 1-3). Each of the three groups has at least one endemic species in South Africa, and Sialidae and Chauliodinae each have endemic species in Madagascar. No megalopterans are known from other parts of sub-Saharan Africa. An endemic sialid species is known from southern Asia, as well as five genera of Corydalinae and four genera of Chauliodinae. In the U.S.S.R. and Europe only *Sialis* occurs today, although fossil evidence indicates that Corydalidae was previously present.

In the Australian Region, two endemic groups of Sialidae occur in Australia. One additional genus of Chauliodinae, *Archichaulidoes* is confined to Australia, New Zealand and Chile.

The Neotropical Region contains endemic sialid species formerly placed in *Protosialis,* as well as a very distinctive Chilean species, *Protosialis chilensis.* This region also shares two endemic genera of Corydalinae and two genera of Chauliodinae with the Australian Region.

The only other genus of Corydalinae found in the Neotropical Region, *Corydalus,* as well as the chauliodine *Protochauliodes,* may provide clues to the largest anomaly of the Gondwanian distribution pattern. *Corydalus* is not only found throughout South and Central America, but also occurs throughout most of North America as well. However, as Glorioso pointed out, "Because of the diversity and presence of the most primitive species of *Corydalus* and *Playneuromus* in the Amazonian region, I hypothesize this as the ancestral range of the common ancestor of these genera, with subsequent range extension into Central America." (p. 273). To this could also be added the genus

Chloronia (Penny & Flint, 1982). *Protochauliodes* has a broad distribution, which may be explained in a similar manner. In addition to being found in Australia, New Zealand, and Chile, it is also present in the western United States. This genus probably has moved northward from its previous Gondwanian distribution. The Chauliodinae also contain four other genera that are endemic to North America. As indicated by the distribution of *Corydalus* and *Protochauliodes,* there appears to have been a pathway for northward movement from South America into the western United States. However, this pathway was probably of early origin, as primitive chauliodine eggs have been found in Tertiary deposits of the Laramie Formation. Thus, the western Nearctic Region may have become a secondary center of evolution within the Chauliodinae at a relatively early date.

This theory of Gondwanian distribution would have to hypothesize a few other factors. Corydalinae would have had to become extinct in Madagascar and Australia. The geographical pattern of *Sialis* would be best explained by a Laurasian, rather than Gondwanian evolution, perhaps from an earlier vicariant event. It should also be noted that the higher classification of Sialidae is badly in need of revision. Such a study could affect the zoogeographical analysis of this family.

The cladogram generated in this study provides another anomaly to a Gondwanian distribution. Although the majority of genera fit well into such a pattern, such as the three South American genera and two primitive lineages in southern Asia, the presence of *Chloroniella* in South Africa in this scenario necessitates either a later evolution of this genus or a movement of an ancestral *Chloroniella* from Asia and into southern Africa. As mentioned earlier, there are no megalopterans today in tropical Africa, and an early extinction with subsequent reintroduction from Asia seems doubtful. A non-parsimonious cladogram, with *Chloroniella* evolving from a position completely compatible with what we know of plate tectonics, is presented in Cladogram 2. In this case, all five Asiatic genera are together at the base of the cladogram. Some of these five genera in three clades could have either been present in southern Asia from a previous vicariant event (perhaps the split of Laurasia and Gondwanaland), or been present as a single or multiple ancestor on the Indian subcontinent as it drifted northward, later forming the genera *Protohermes, Neurhermes, Neoneuromus, Neuromus,* and *Acanthacorydalis.* As the continents of Africa and South America separated, they took with them the ancestors of *Chloroniella,* and *Platyneuromus, Chloronia,* and *Corydalus,* respectively. Although not the most parsimonious cladogram, there are only four more steps (113 steps; consistency index 0.664) than the most parsimonious cladogram, and in view of the general
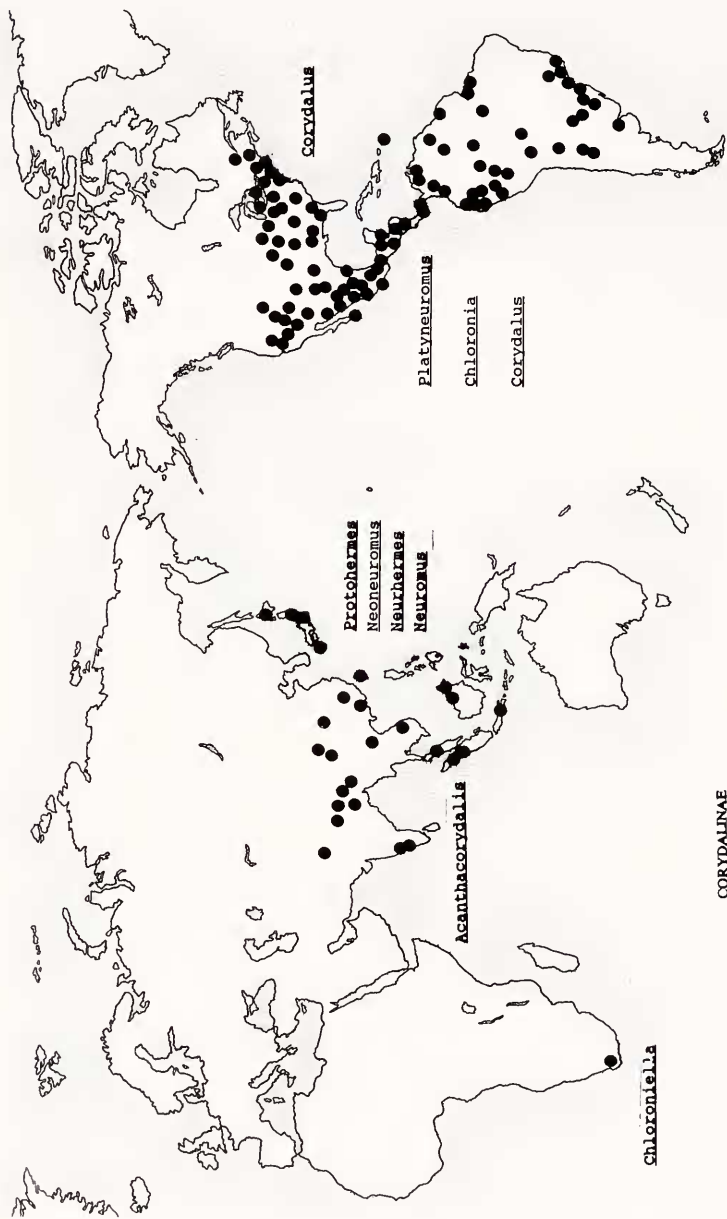
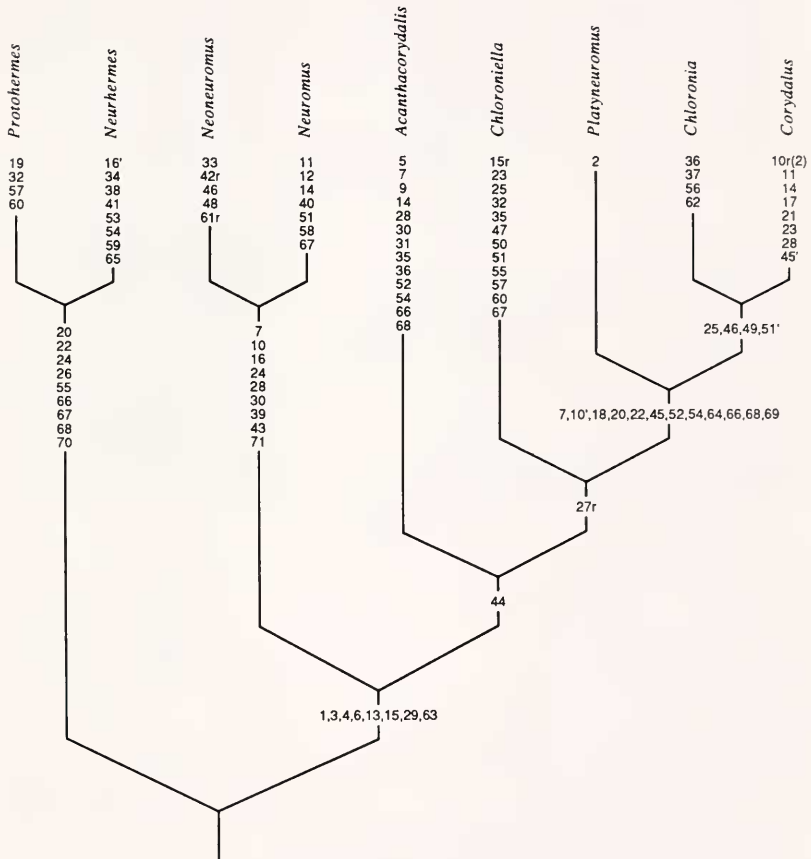Map 1. Geographical distribution of the genera of Corydalinae.
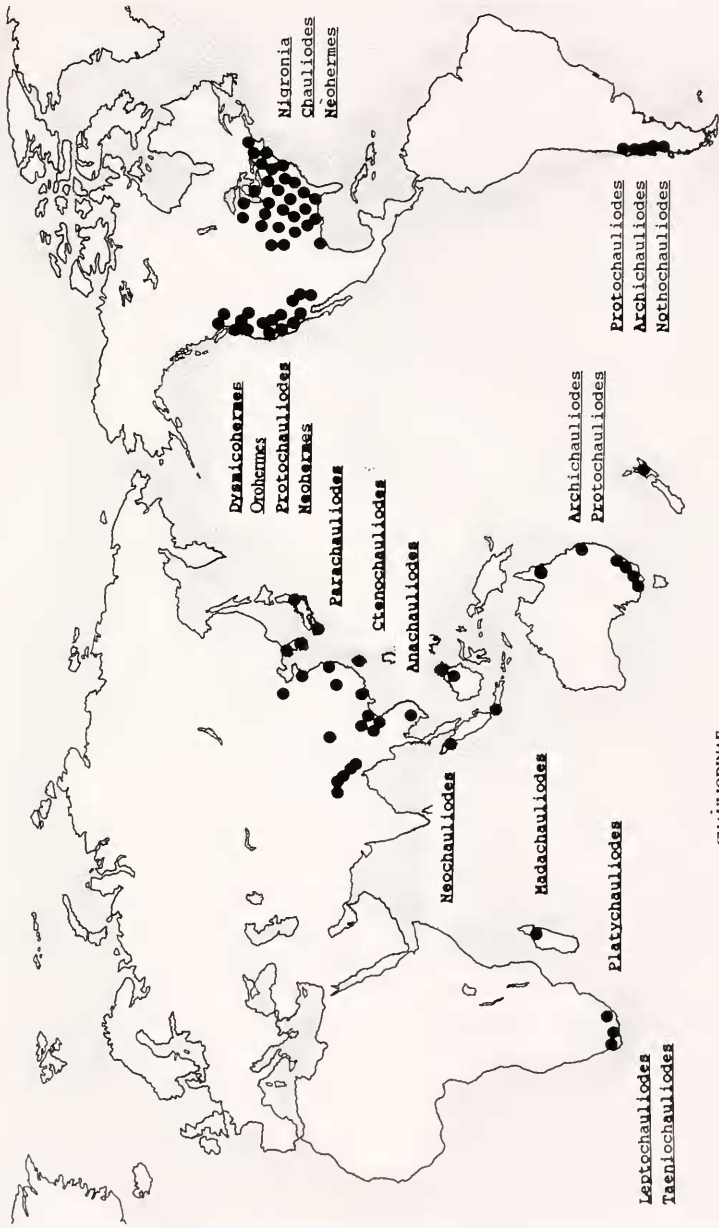
Map 2. Geographical distribution of the genera of Chauliodinae.
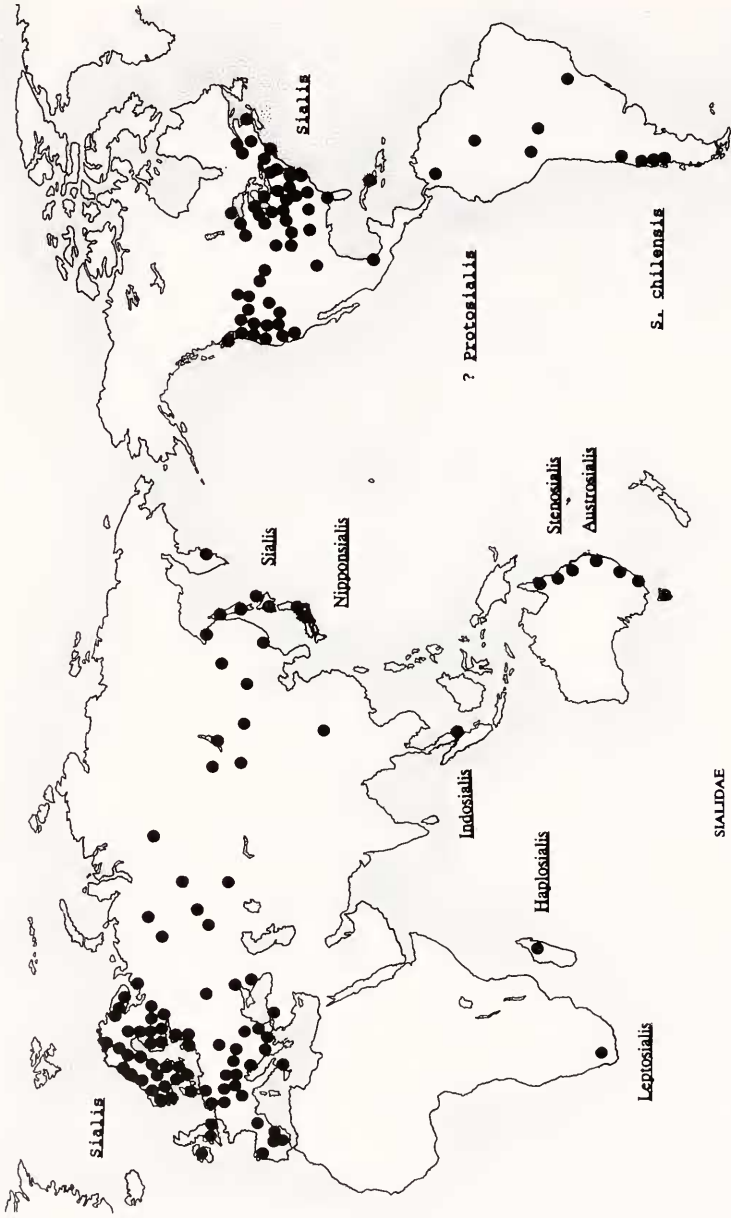
Map 3. Geographical distribution of the genera of Sialidae.

indications of a Gondwanian distribution, it is felt that this non-parsimonious modification is justified.

Because of similar biologies and restrictions to fresh water environments, the three main groups of megalopterans may have had similar histories of speciation and vicariant events. Much of this early evolution may have been caused by plate tectonics, leading to the similar world-wide distribution patterns evident today. Further studies of sialid and chauliodine phylogeny may reveal whether geographically associated

CLADOGRAM 2

Cladogram 2. Phylogenetic position of corydaline genera reflecting geographical distributions.

genera of the three groups had similar cladistic histories, or not. They
may also reveal which of the two cladograms presented best fits a general
megalopteran evolution pattern.

Table 1. Characters of the Corydalinae with their plesiomorphic and apomorphic
states.

Character	Plesiomorphic	Apomorphic
1. Head shape	Robust	Flattened
2. Postocular flange	Absent	Present
3. Postocular spine	Feebly developed	Moderately to well developed
4. Posterior tentorial pits	Linear	Arcuate
5. Cranial disk	Without spines	With spines
6. Antennae	Feebly subserrate	Filiform
7. Clypeal margin	Entire	Incised medially
8. Male mandibles	Not enlarged	Enlarged
9. Female mandibles	Three-fourths head length or shorter	Length of head
10. Labrum shape	Triangular	Ovoid
10'.		Broadly truncate
11. Labral position	Over mandibles	Between mandibles
12. Labral anterior margin	Sparsely setose	Fimbriate
13. Maxilla shape	Short and broad	Relatively elongate
14. Lacinia apex	With three elongate setae	Without elongate setae
15. Galeal setae	Flattened, lanceolate	Bristlelike
16. Galeal sensory peg	Well developed	Poorly developed
16'.		Absent
17. Maxillary palp	Five-segmented	Four-segmented
18. Maxillary palp apex	Conical	Broadly rounded
19. Maxillary palp setae	Long	Short
20. Maxillary palp sensory areas	One at apex	Two at apex
21. Labial palp	Four-segmented	Three-segmented
22. Labial palp sensory areas	one at apex	Two at apex
23. Last branch of radial sector	Bifurcate	Not bifurcate
24. M1 + 2 branches	Two	Four or more
25. M3 + 4 branches	Two	One
26. 1A branches	Two	Three
27. R1-Rs crossveins	Three	Four or more
28. Medial crossveins	Two	Three or more
29. M-Cu crossveins	Three	Four
29'.		Six or more
30. Cubital accessory crossveins	Absent	Present
31. Costal crossveins	Vertical or oblique	Reticulate
32. Male ninth sternum	Hind margin not notched	Hind margin notched
33. Male ninth sternum	More or less quadrate	Attenuate

Table 1. Character states *(continued)*

Character	Plesiomorphic	Apomorphic
34. Male ninth sternum	Without median projection	With median projection
35. Male ninth sternum	Without posterolateral lobes	With posterolateral lobes
36. Male ninth sternum	Without setiferous lateral protuberances	With setiferous lateral protuberances
37. Male ninth sternum	With normal setae	With short, stout setae
37'.		With fine setae
38. Male ninth sternum	Not sclerotized dorsally	Sclerotized dorsally
39. Male ninth sternum	Without internal ridges	With internal ridges
40. Male ninth sternum	Not locking with tenth sternite	Locking with tenth sternite
41. Male ninth tergum	More or less quadrate	Short, with broad median incision
42. Male ninth tergum	With dorso-lateral incisions	Without dorso-lateral incisions
43. Ninth tergal internal inflection	Without median fossa	With median fossa
44. Ninth tergal internal inflection	Arched	Inverted V-shaped
45. Membrane between 9th & 10th sternites	Thin	Thickened, bilobate
45'.		Thickened, regularly convoluted
46. Genital papillae	Present	Absent
47. Genital papillae medially	Separated	Fused
48. Tenth gonocoxites	Without median projection	With median projection
49. Tenth gonocoxites	Antero-lateral corner without acute projection	Antero-lateral corner with acute projection
50. Tenth gonocoxites	Medially joined	Medially separated
51. Tenth gonostylus	Digitiform	Short, broad
51'.		Papilliform
52. Ninth gonostylus	Unguiform	Clavate
53. Ninth gonostylus	Relatively short	Long, bent
54. Ninth gonostylus	Sparsely setose	Densely setose
55. Ninth gonostylus apodeme	Parallels ninth tergum	Directed medially
56. Tenth tergites	Short	Long, thin
57. Tenth tergites	Without sensory field on apical surface	With sensory field on apical surface
58. Tenth tergites	Rounded	Laterally compressed
59. Tenth tergites	Uniramous	Biramous
60. Tenth tergites	Not bearing basal tuft of hairs	Bearing basal tuft of hairs
61. Eleventh tergum	Present	Absent
62. Lateral sclerite of ovipositor	Well sclerotized	Weakly sclerotized

Table 1. Character states *(continued)*

Character	Plesiomorphic	Apomorphic
63. Gonostylus	Articulated with gonocoxite	Fused with gonocoxite
64. Sternal pouch	Absent	Present
65. Sclerites between 8th sternum & gonopore	Absent	Present
66. Bursa copulatrix	Not saclike	Saclike
67. Number of spermathecae	Two	One
68. Spermathecal duct	Continuous with bursa	Separate from bursa, T-shaped
69. Accessory glands	Present	Absent
70. Accessory glands	Short	Long
71. Accessory glands	Sigmoid	Linear

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